VISUAL FORM DISCRIMINATION BY ECHOLOCATING BATS

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Visual information is generally thought to be of little importance to echolocating bats, many of which exhibit a great diversity in their diets and behavior. Although all apparently rely heavily on acoustic orientation, one might expect that non-auditory senses such as vision and olfaction could provide valuable supplements to audition in the performance of certain activities. Visual pattern perception could also aid in homing and long distance navigation if celestial bodies or landmarks beyond the range of echolocation can be seen.

A number of tropical species possess relatively prominent eyes which may aid them in finding fruit, nectar or in the case of vampires, large mammals. However, previous experiments have failed to demonstrate pattern vision. Eisentraut (1950) succeeded in conditioning *Eptesicus serotinus* and *Plecotus auritus* to distinguish white from black cards or doorways by rewarding proper choices with food but was unsuccessful in an attempt to train them to discriminate between a cross and a circle. Curtis (1952) similarly conditioned *Myotis lucifugus* and *Eptesicus fuscus* to search for food at the light, rather than dark end of a test chamber, but these bats did not distinguish between stripes subtending one and eight degrees. Light-dark discrimination has also been shown for *Myotis sodalis* (Davis and Barbour, 1965). The results of these and other experiments supported the supposition that the Microchiropteran eye was probably able to do little more than distinguish light from dark. Suthers (1966; in press) however, obtained optomotor responses to moving stripes suggesting minimum separable angles of less than one degree in some species. Bradbury and Nottebohm (in press) and Chase and Suthers (1969) demonstrated that deafened *Carollia perspicillata, Phyllostomus hastatus* and *Myotis lucifugus* can visually detect and avoid obstacles placed in their flight path. Vision has, in fact, recently been implicated as an aid to orientation during homing (Williams and Williams, 1967).

In this paper we present evidence that at least two species of Microchiroptera are able to distinguish visually between simple stationary patterns. Of these, *Anoura geoffroyi* (Gray) is nectivorous and *Carollia perspicillata* (Linnaeus) is frugivorous. Both are nocturnally active and emit ultrasonic cries which they use in echolocation.

METHODS

A hungry bat was conditioned to seek food at one member of a pair of equal area patterns presented simultaneously as silhouettes against a diffusely trans-illuminated background. One pattern was always associated with edible food (serving as positive reinforcement), whereas the other was associated with a
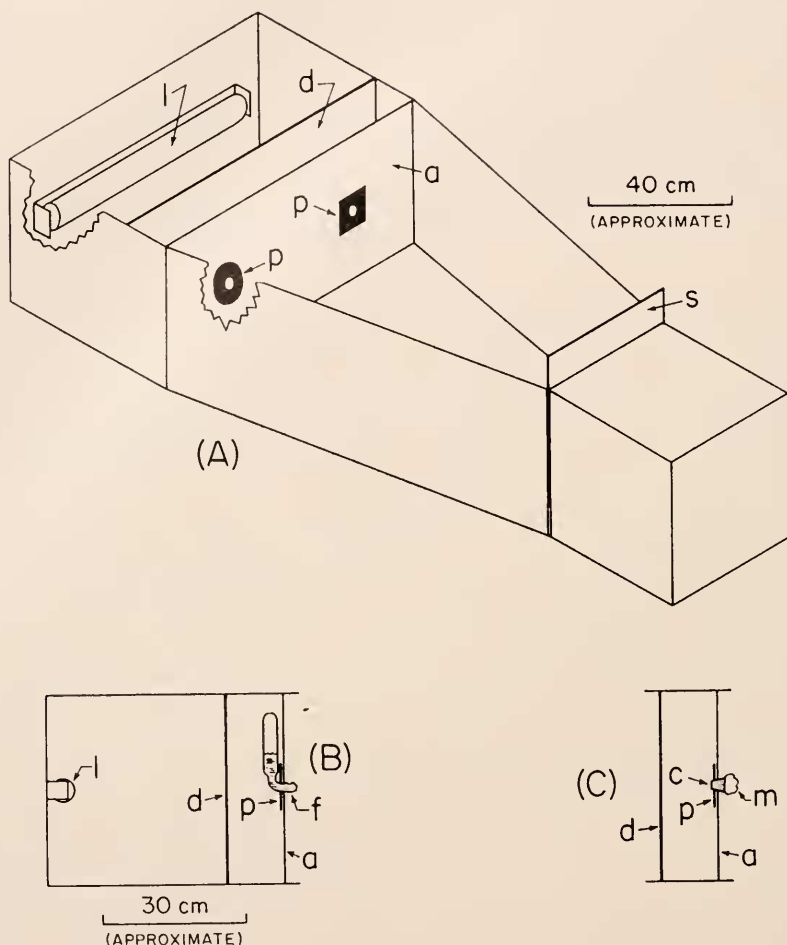
FIGURE 1. A. Conditioning apparatus used for *Anoura geoffroyi* and *Carollia perspicillata*. B. Detail (side view) showing dispenser with sucrose or control solution as presented to *A. geoffroyi*. C. Detail (side view) showing manner in which melon ball was presented to *C. perspicillata*. a, clear acrylic plastic sheet; c, cork with peg holding melon ball; d, translucent diffusing plate of frosted glass; f, glass fluid dispenser used with *A. geoffroyi*; l, fluorescent or incandescent light bulb; m, melon ball; p, patterns; s, starting point for bat at beginning of each trial.

distasteful aqueous quinine solution or quinine-treated food (serving as negative reinforcement) or with no food.

Anoura and *Carollia* were tested in a plywood box with an open top covered by wire mesh (Fig. 1a). Both of these genera are capable of stationary, hovering flight and flew easily within this chamber. The *Carollia* to be tested was isolated behind a removable, opaque partition 105 cm from the test patterns. On the other side of this partition the chamber gradually widened toward a 78 × 30 cm sheet of clear acrylic plastic. The test patterns were constructed of heavy, opaque, black

poster cardboard and mounted on the back of this clear plastic sheet with their centers 40.5 cm apart. A frosted glass diffuser panel of similar dimensions was mounted 10 cm behind the clear plastic, parallel to it. A 20 watt white fluorescent bulb centered 30 cm behind this diffuser provided an illuminance of about 50 apparent foot-candles on the plastic surrounding the patterns. Positive or negative reinforcement was provided at the center of each pattern through an 18 mm diameter hole in the plastic and cardboard. The relative positions of the two patterns were interchanged semi-randomly between trials. The transparent plastic sheet between the bat and the cardboard pattern prevented echolocation of the latter.

At the beginning of each trial the partition isolating the bat from the patterns was raised and the animal was allowed to fly toward the patterns. The bat was considered to have made a choice when it touched the edible or quinine-treated food, or their dispensers. A trial was termed a success if this first contact occurred at the positively rewarded pattern. Contacts at either pattern were usually accompanied by tasting or eating. Sometimes the bat flew on a nearly straight line directly to one of the patterns as soon as the partition was raised. Often several flights were made near one or both patterns before the animal attempted to eat at one of them. When a high per cent of correct choices indicated conditioning had taken place, control trials were randomly interspersed during which identically treated edible food or pure water was placed at both patterns in order to establish that choices were based on visual rather than possible olfactory clues. Prior to each olfactory control trial, the surface of the plastic sheet was thoroughly washed to remove odors.

FIGURE 2. Pattern pair consisting of disc and equal area rectangle. *Anoura geoffroyi* was conditioned to seek food at the disc.

A test chamber of slightly different dimensions was used during the disc *vs.* rectangle experiments with *Anoura* (Fig. 2). The patterns were spaced 30 cm apart on a 60 × 30 cm sheet of clear acrylic plastic which was trans-illuminated by two 15 watt incandescent bulbs behind a sheet of frosted glass. The illuminance at the surface of the clear plastic was about 200 apparent foot-candles (*i.e.,* assuming a human phototopic luminosity curve for the bat). The reward consisted of an approximately 1 molar aqueous sucrose solution. Negative reinforcement was provided by an aqueous quinine solution. Each solution was presented in a glass water dispenser mounted behind the pattern with its delivery spout extending about 2 cm into the test chamber through a hole at the center of the pattern. Several dispensers were used and occasionally interchanged to prevent the bat from associating any minor peculiarity in the shape of a particular feeder with the sucrose or quinine. *Anoura* fed by hovering in front of the dispenser and extending its long tongue into the fluid (Fig. 3).

Another *Anoura* was later tested on triangles, squares, and discs in a similar box (Fig. 4). The opaque partition in this apparatus was 137 cm from the test patterns which were mounted 40.5 cm apart on a 78 × 53 cm sheet of clear plastic.

FIGURE 3. *Anoura geoffroyi* hovering in front of pattern while drinking from feeder. Note long tongue extending into sucrose solution.

A 20 watt white fluorescent bulb was centered 42 cm behind the frosted glass diffuser. Water dispensers protruded through holes in the clear plastic immediately below each pattern rather than at its center.

During experiments with *Carollia*, each glass feeder was replaced by a melon ball (*ca.* 2.5 cm in diameter) attached to a cork which fitted into the hole at the center of each pattern. Commercially available frozen melon balls were thawed and washed in water to remove excess packing syrup. Some were then soaked in an aqueous sucrose solution to be used as positive reinforcement; others were soaked in an aqueous quinine-sodium chloride solution to serve as negative reinforcement. Since the melon balls were somewhat irregular in shape, they were periodically replaced during each series of trials to prevent the bat from associating a particular one with reward or punishment. Olfactory controls were accomplished by occasionally placing sucrose treated melon balls at both patterns after washing the surface of the plastic.

RESULTS

Anoura geoffroyi

Our first experiments were conducted with this nectivorous bat. The animal was allowed to become accustomed to the test chamber by feeding in it for a few days prior to the presentation of patterns. The first pattern pair consisted of a postively rewarded ring and a negatively reinforced cross with the sucrose and quinine dispensers situated a few centimeters in front of the patterns. This distance was apparently enough to make it difficult for the bat to associate the feeder with the pattern. During nine days of experiments the animal's score occasionally approached statistical significance but fluctuated too much from day to day for a clear result to be obtained. The apparatus was then redesigned so that a feeder projected directly out of the center of each pattern as described above.
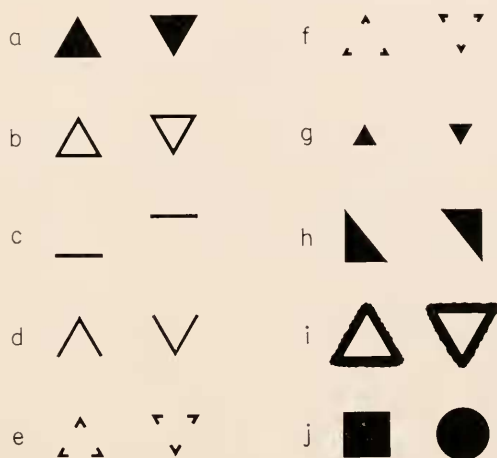

FIGURE 4. Pairs of patterns used in analysis of discrimination between erect and inverted triangles by *Anoura geoffroyi*. See text.

Disc vs *rectangle* Simultaneously with the rearrangement of feeder position the test patterns were changed to a solid disc 73 mm in diameter and a long, narrow vertical rectangle (15 × 280 mm) of equal area (Fig. 2). Sucrose was associated with the disc, quinine with the rectangle. Conditioning took place rapidly and after 51 trials in two days the animal consistently made more than 70 per cent correct choices. During the next three successive days, this specimen of *Anoura* chose the sucrose solution in 83.1 per cent of 89 trials ($P < 0.01$) and in 100 per cent of eight olfactory control trials ($0.01 < P < 0.02$) in which only water was present at both patterns. The bat's performance improved each day until on the final day of testing it scored 92.9 per cent correct choices in 28 trials. The rapidity with which this discrimination was learned may be misleading, however, since there could have been some transfer from the ring used in the initial tests to the disc.

Analysis of discrimination between erect and inverted triangles We subsequently tested a second specimen of *Anoura* with a view to determining what aspects of simple patterns are utilized in their visual discrimination and also in

TABLE I

Visual form discrimination and transfer of learning by Anoura geoffroyi

Pattern pair	Number of trials	Per cent successes	Value of P
a	92	83.7	<0.01
b	17	88.2	<0.01
c	15	93.3	<0.01
d	15	53.3	~1.0
e	15	86.7	<0.01
f	20	70.0	<0.20
g	32	68.7	<0.10
h	15	86.7	<0.01
i	10	50.0	<0.80
j	15	93.4	<0.01

order to obtain a more direct comparison of the visual form discrimination of a bat with that of some other non-ecolocating mammal. This comparison was facilitated by using patterns similar to those which Lashley (1938) presented to rats.

An *Anoura* was trained to visually distinguish between a pair of identical equilateral triangles measuring 10 cm on a side. One triangle was erect, the other inverted (Fig. 4a; Table Ia). Sucrose solution was associated with the erect triangle and a quinine solution with the inverted triangle. In all experiments with this bat, the position of the patterns was determined from Gellerman's (1933) table of trial orders to avoid scores due to position habits, simple alternation, and double alternation. The first five days of testing (90 trials) during which the bat was being conditioned are not included in Table I. Olfactory controls using sucrose solution at both patterns were performed with every pair of patterns and are included in the trials of Table I. When the value of P for the non-olfactory control trials was less than 0.05, the value for olfactory control trials was also less than 0.05. In no case was there evidence that choices were being made on the basis of olfactory stimuli.

After *Anoura* was conditioned to seek food at the solid, erect, equilateral triangle we confronted it with other pattern pairs selected in an effort to determine upon what specific aspects of the triangles, pattern discrimination depended. If the conditioning transferred to the new patterns, it could be assumed they retained a distinguishing characteristic of the original pair of triangles. Such transfer test patterns were presented to the bat on only one night for from 10 to 32 successive trials—nearly all of which were olfactory controls. On the night following each such test for transfer of conditioning the bat was retested for about 10 trials on the original equilateral triangles.

From Table I and Figure 4 it can be seen that this *Anoura* which was trained on solid equilateral triangles (a) transferred its conditioning to the complete outlines (b) of these triangles and to the baseline (c) of each triangle presented above, but not to the two sides without a base (d). When the corners of the triangles were presented, *Anoura* was able to choose correctly if the side segment forming each corner extended 1.5 cm from the inside angle (e) but not when this length was reduced to 1 cm (f). Small solid equilateral triangles measuring 5 cm on a side (g) were distinguished on only 68.7 per cent of the trials. Conditioning

to equilateral triangles transferred to right triangles (base 9 cm, height 11 cm) (h). The bat's score fell to a chance level when the contrast was reversed so that translucent equilateral triangles 10 cm on a side appeared in a black surrounding (i). Initial trials prior to conditioning are omitted from Table Ia but are included in the learning curve in Figure 5.
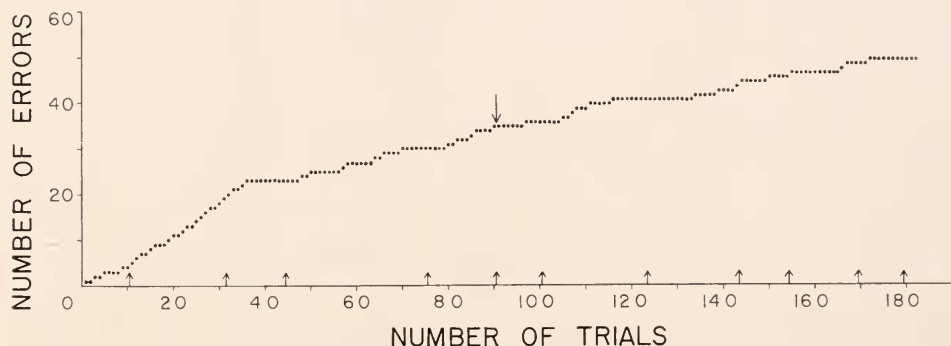

FIGURE 5. Learning curve of *Anoura geoffroyi* for erect and inverted equilateral triangles 10 cm on each side. Upward pointing arrows along abscissa indicate successive days of testing. Large arrow touching curve between fifth and sixth day indicates beginning of trials included in Table I. Learning may be considered to have occurred as early as the third day, depending on the criterion used.

These data suggest that *Anoura* depended almost exclusively on the baseline of the pattern for making its choices. Failure to differentiate between members of pair (f) may be explained as due to the less complete baseline in comparison to (e) or possibly to an excessive demand upon the animal's visual acuity. Failure in the case of pair (g) is difficult to understand unless it is due to the shortness of the baseline relative to that of the training patterns.

Immediately following the preceding experiments involving triangles the same bat was confronted with a 10×10 cm square above the sucrose solution and an equal area (11.2 cm diameter) disc (j) above the quinine solution. The conditioning to the equilateral triangles also transferred to this pair of patterns. The square was selected in 93.4 per cent of 15 trials on the first night of its presentation. The only error was made on one of eleven olfactory control trials included in the above total ($P < 0.01$ for all trials; $0.01 < P < 0.02$ for olfactory controls). The base of the square was in the same position and orientation as the base of the erect triangle and must have been the basis of its selection by the bat. Since the top of the square similarly resembled the base of the inverted triangle, the success of the bat suggests that it no longer heeded the negative pattern and relied exclusively on the presence of a positive pattern baseline. This test was performed after 28 days of testing on the other patterns in Figure 4. It is interesting to note that this reliance on the baseline of the positive triangle apparently developed to the exclusion of other aspects of the pattern pair only after many days of conditioning. Thus when the same bat was presented with the same square and circle, each with sucrose solution, after 18 days of conditioning there was no transfer, the correct choice occurring on only 42.9 per cent of 14 trials.
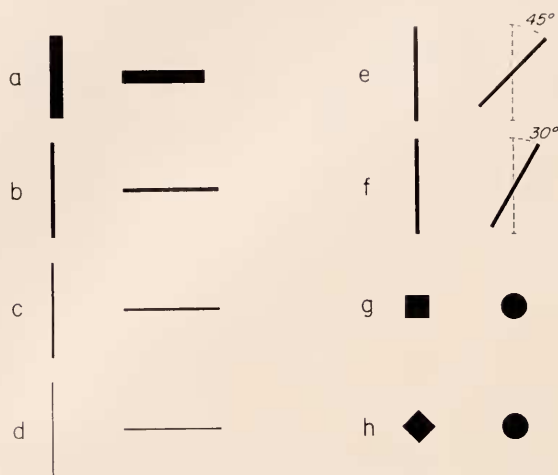
FIGURE 6.   Pairs of equal area patterns presented to *Carollia perspicillata*.
Scale is approximate.   See text.

Carollia perspicillata

One *C. perspicillata* learned to distinguish between two identical rectangular stripes—a vertical one associated with food and a horizontal one associated with quinine (Fig. 6).   During the first series of experiments 40×243 mm rectangles (a) were used.   In three successive experiments the length of these rectangles was increased to 280 mm and their width was reduced to 14 (b), 7 (c), and finally 3.5 mm (d), respectively.   Trials prior to conditioning on the 40 mm wide rectangles are not included in line (a) of Table II.   Once the bat learned to distinguish between the vertical and horizontal member of this pair the animal maintained its performance when presented with 14 or 7 mm wide rectangles. Specimens of *Carollia* scored about 90 per cent correct choices with these three wider pairs of rectangles.   The slight improvement in performance with 14 and 7 mm wide rectangles is probably simply the result of additional training, since there was good transfer of learning between these pairs.   One may alternatively

TABLE II

Visual form discrimination by Carollia perspicillata

Pattern pair	Number of trials	Per cent successes	Value of P
a	95	89.5	<0.01
b	65	92.3	<0.01
c	60	93.3	<0.01
d	85	52.9	$0.50>0.70$
e	108	75.0	<0.01
f	298	68.5	<0.01
g	75	80.0	<0.01
h	40	90.0	<0.01

hypothesize that the narrower the rectangles the more strongly was their contrasting orientation emphasized and that this facilitated correct choices by the bat. When the width of the rectangle was further reduced to 3.5 mm, the score abruptly dropped to about the 50 per cent predicted by chance selection. When trials with wider rectangles were inserted between those with these narrowest rectangles, the bat readily made the correct choices—indicating the poor performance on the 3.5 mm wide rectangles was not due to a lack of motivation, but probably instead to excessive demands on the bat's acuity or perhaps simply to a decreased conspicuousness of patterns that remained visible.

The same *Carollia* was subsequently presented with a pair of 14×280 mm rectangles in which the postively reinforced member of the pair was oriented vertically as before, but the long axis of the negatively reinforced rectangle formed an angle of 45 (and, in later experiments, 30) degrees with the vertical (Fig. 6e and f; Table II). Although the bat's performance progressively diminished as the long axis of the negative rectangle was rotated toward the vertical orientation of the rewarded pattern, even when this difference was reduced from 90 to 30 degrees, the *Carollia* scored nearly 70 per cent correct choices.

A second *Carollia* demonstrated an impressive ability to distinguish between a solid square, 7 cm on each side, and an equal area solid disc with a diameter of 7.8 cm (Fig. 6g and Table II). When this square was rotated 45 degrees so that it appeared to stand on one corner (Fig. 6h) the bat continued to make the distinction without having to relearn the problem. This indicates that *Carollia* must indeed discriminate between these patterns on the basis of their shapes—the corners and straight edges of the square contrasted to the curved edge of the disc—and not on the basis of small spatial differences in illumination which must exist even though the average luminous flux is the same around each pattern.

Discussion

Limited data on the visual acuity of twelve echolocating bats was obtained by Suthers (1966 and in press) on the basis of optomotor responses to moving stripes. *Anoura geoffroyi* and *Carollia perspicillata* responded to stripes subtending 0.7 and 0.5 degrees, respectively.

The present experiments do not provide data on visual acuity since there was no fixed distance at which the bat was forced to make a decision. Attempts to force *Anoura* to make a choice at a predetermined distance from the patterns were unsuccessful. Neither could a consistent choice point be determined by tracing the bat's flight path towards the patterns. Although conditioned animals often seemed to fly directly to the correct pattern, the point at which their flight deviated to the left or right was difficult to determine since the initial portions of even direct flights were very similar. At other times the bat would approach to within a few centimeters of first one pattern and then the other before choosing. The narrow stripes of Figure 6d may have placed excessive demands on the acuity of *Carollia*. However, the bats should have been able to resolve the major features of the other patterns used.

The subordinate role of vision as a telereceptive sense is indicated by the fact that our experimental animals resorted to visual stimuli only after failing to obtain a reliable indication of the position of the food through place learning, echoloca-

tive or olfactory stimuli. Similar behavior has been noted in other "nonvisual" animals and it is interesting to compare the visual form discrimination of bats with that of a non-ecolocating nocturnal mammal. One of the nocturnal mammals most thoroughly studied in this respect is the rat. Our experiments testing the ability of *Anoura* to transfer discrimination from triangles to other patterns are similar to some of those conducted by Lashley (1930, 1938) and Munn (1930) with pigmented rats. Visual pattern discrimination experiments using the rat are summarized by Munn (1950).

Rats are similar to bats in having nocturnally adapted eyes with all or nearly all rod retinae lacking a fovea. Rats which Lashley and Munn trained to discriminate between erect and inverted equilateral triangles transferred to triangular outlines. Most rats transferred to two sides, some transferred to the bases alone, and about one-tenth of the rats tested responded to the lower angles. Large changes in the size of the equilateral triangles or the substitution of right triangles did not affect the performance of the rat (Fields, 1932). Reversal of contrast, however, destroyed the rat's ability to discriminate. Rats are apparently unable to distinguish between equal area squares and circles. Allowing for some individual variations, it appears that *Anoura geoffroyi* is capable of form discrimination at least comparable to that of pigmented rats. In contrast to rats, all of our bats were able to distinguish between squares and equal area circles, suggesting that their form perception may be in some respects superior to that of rats.

Tests showing transfer of form discrimination raise the question as to whether or not the animal possesses an abstract concept of form such as triangularity (see Fields, 1932). In the absence of such a concept, form discrimination may depend on a particular retinal distribution of light or the relationship of a pattern to its surroundings. The fact that a specimen of *Anoura* transferred from equilateral triangles to three corners and to right triangles suggests it may have had some awareness of triangularity. This interpretation is cast in doubt, however, by the animal's transfer to horizontal rectangles representing the base lines of triangles. The successful transfer by *Carollia* to a rotated square (Fig. 6h) could be interpreted to imply some degree of abstraction of the concept of squareness or circularity by this bat but further careful experiments are needed. Such abstractions, as pointed out by Lashley (1938), should probably be considered as evolutionary refinements of the fundamental capacity for generalization rather than as unique or sudden evolutionary advances.

The ability for form discrimination has been studied in a number of other animals, but the variety of patterns presented and experimental techniques employed make a meaningful comparison difficult. Karn and Munn (1932), however, conditioned two mongrel dogs to distinguish between erect and inverted equilateral triangles and found that they transferred not only to complete outlines, the three corners, and the baseline, but also to the two sides without a baseline. Since *Anoura* did not treat this latter pattern as equivalent to the original triangle, bats and dogs may differ in the means by which they perceive these forms. Sutherland (1957) has hypothesized a mechanism of form discrimination based on extensive experiments with the octopus (*Octopus vulgaris*). He suggests that the octopus visual system may distinguish between forms on the basis of their vertical and horizontal extents or projections. The pattern pairs which we presented to our

bats did not include critical experiments to test this hypothesis for these animals. The ability of *Anoura* to distinguish between identical horizontal bars representing the bases of triangles (Fig. 4c) and its inability to discriminate between the sides of erect and inverted triangles (Fig. 4d), however, suggests that the Microchiropteran visual system must utilize more than these two aspects of forms in making a discrimination. Different mechanisms of form discrimination in these animals would not be surprising considering the phylogenetic remoteness of bats from cephalopod molluscs.

Why should a bat which has evolved a sophisticated capacity for echolocation also maintain a comparatively good visual system? The answer may lie in the relatively limited range of effective echolocation due to atmospheric attenuation and spreading losses of sound. Visual recognition of large objects or landscapes beyond the range of echolocation may assist echolocating bats in orienting themselves on long distance flights to feeding trees or sites. *Phyllostomus hastatus* apparently use visual orientation to home from distances greater than about 10 km (Williams, Williams and Griffin, 1966; Williams and Williams, 1967). Chase and Suthers (1969) and Bradbury and Nottebohm (in press) obtained evidence that *Carollia, Phyllostomus,* and *Myotis* are able to visually detect and avoid certain stationary obstacles during flight. Although Microchiropteran eyes are some what hypermetropic, this refractive error is probably insignificant compared to the total power of the eye and their great depth of field probably compensates for the absence of a well developed accommodative mechanism (Suthers and Wallis, in preparation). Vision is certainly a functional, if secondary sense of echolocating bats. Its importance varies with the species' behavior and ecology.

Summary

Two species of echolocating Microchiroptera were behaviorally conditioned to visually discriminate between various pairs of simple, equal area patterns presented simultaneously as silhouettes against a diffusely trans-illuminated background. These were *Carollia perspicillata* (frugivouous) and *Anoura geoffroyi* (nectivorous). Data suggest that visual form discrimination in bats such as *Anoura geoffroyi* is comparable or superior to that demonstrated in pigmented laboratory rats. Pattern vision may supplement or replace acoustic orientation in the detection of relatively large distant objects where the propagation losses of ultrasonic cries seriously reduce the echo intensity. Vision may be an important aid to navigation of bats on feeding or migratory flights.

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